

AGONISTIC BEHAVIOR IN THE AMERICAN GOLDFINCH¹

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THE term "agonistic behavior," used here in its strict sense, includes both aggressive and submissive displays. This behavior has been observed in the American Goldfinch (*Spinus tristis*) by several authors, but there is little agreement among them. Some have indicated that agonistic behavior occurs in connection with territoriality and defense of nest sites (Drum, 1939; Batts, 1948; Roberts, 1942; and Stokes, 1950). Others, including Sutton (1959) and Walkinshaw (1933), have not observed agonistic encounters, and Sutton describes disputes over nesting territories as "playful." The present investigation of the American Goldfinch seeks to clarify these conflicting viewpoints. It includes a description and analysis of movements, calls, and displays involved in agonistic behavior, and a discussion of its influence on social hierarchy and territoriality.

MATERIALS AND METHODS

Field work was conducted at or near the University of Michigan Biological Station, Pellston, Michigan during the summer of 1961, and at the Edwin S. George Reserve near Pinckney, Michigan in the summer of 1962. Wild birds were studied with 7×50 binoculars, since most individuals quickly became accustomed to the presence of a human being nearby. Approach to within ten or twenty feet was possible without noticeable changes in normal behavior patterns.

In August, 1961, five nestling goldfinches (two males and three females) were captured near the University of Michigan Biological Station. The birds were about ten days of age when taken from the nest and were hand-reared on a "paste" composed of boiled egg yolk, pablum, and milk. After being confined to a small cage ($50 \times 50 \times 60$ cm) during August and September, they were moved to a flight cage ($1 \times 1 \times 1.3$ m) on 1 October. Observations of agonistic behavior were made on this group of birds until 11 April 1962. At this time, a male and female were separated from the rest of the birds and placed in a small cage ($50 \times 50 \times 50$ cm) for the duration of the breeding season.

DISPLAYS

Head-up.—In the Head-up Display, the bird faces its opponent with neck slightly extended, body feathers neither fluffed nor sleeked, and legs extended somewhat (Fig. 1). This posture is maintained for one or two seconds and is

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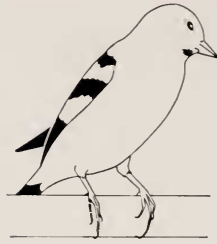


FIG. 1. Head-up Display showing mild aggression.

often given by the victor just after an agonistic encounter. Since a bird giving this display may either attack its opponent or return to quiet perching, feeding, or preening, the display may be interpreted as showing evidence of a weak tendency to attack.

Carpals-raised.—A slightly more intense display has been observed during which the neck is retracted, the carpal bones are raised as the wrist is rotated outward, and the body feathers are somewhat sleeked (Fig. 2). The legs may or may not be extended, and the beak is sometimes opened. This often results in a posture similar to that of normal perching, but with the primaries held about two millimeters away from the contour feathers. Birds giving the Carpals-raised Display are likely to attack opponents.

Head-forward.—In its lowest intensity, the Head-forward Display involves facing the opponent with legs flexed, neck extended, and beak closed. The body feathers are usually sleeked to some extent and the wings may be rotated slightly as in Carpals-raised (Figs. 2 and 3). If the bird shows a greater tendency to attack, one or both wings are raised, the neck is extended and lowered, and the beak is pointed at the opponent. When only one wing is raised, it is usually the one further from the attacked individuals. The high intensity Head-forward Display is characterized by retracting the neck and raising the wings, during which they are spread and/or fluttered. The beak is

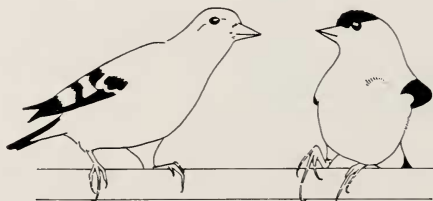


FIG. 2. Agonistic encounter. Note facing of opponent by both birds. Low intensity Head-forward by female to left. Male on right shows Crown-raised and leaning away (fear), Carpals-raised and wing opposite opponent raised (aggression).

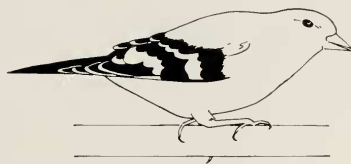


FIG. 3. Low intensity Head-forward (slightly more aggressive than female, Fig. 1), opponent to right. Horizontal posture, feathers sleeked, bird faces opponent with long axis of body directed toward it.

opened, the body feathers are sleeked, the tail is raised slightly and fanned, and the legs are flexed (Fig. 4). In many cases, this action is accompanied by one or two harsh, grating *caws* on the part of the aggressor. This may be followed by hopping or sidling rapidly toward the opponent, the long axis of the body oriented directly toward it. Tail-flicking, during which the closed rectrices are moved rapidly in an arc or circle, often accompanies head-forward displays. Neither the pivoting behavior nor the fluffing of the contour feathers of an attacker, as noted in the European Goldfinch (*Carduelis carduelis*) (Hinde, 1955-56), were seen in the American Goldfinch.

Body contact.—In some cases, aggressive birds pecked at or plucked feathers from other individuals. The pecking was directed toward the point nearest the aggressor, usually the head or side of the attacked individual. This was especially evident in the young captive birds from 30 to 60 days of age. This period marked the first appearance of attacking behavior and it was



FIG. 4. Agonistic encounter. Both birds in extreme Head-forward with wings raised, beaks open. Female to left with wings fluttering, tail fanned, neck withdrawn.

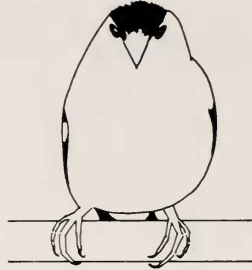


FIG. 5. Submissive posture, aggressor to left. Note leaning away, crown raised, beak pointed downward.

not accompanied by preliminary displays. In this case, it seemed to be initiated merely by the close proximity of other individuals. This spontaneous pecking decreased considerably as the birds matured and is seldom seen in adult individuals. When pecking does occur in adults, it is usually preceded by one of the displays described above.

Supplanting.—The supplanting attack occurs in both wild and captive individuals. The aggressor flies directly toward another bird, alighting in its place or one to two centimeters away. The perched individual almost invariably flies just before the attacker reaches the perch. In some instances, the attacked individual merely moves a few centimeters away along the perch. Flight away from the hostile bird often results in aggressive chases. During these, the submissive individual is supplanted as soon as it alights, being chased rapidly from perch to perch. This may be continued for several seconds until the aggressor perches quietly or the chased individual refuses to fly.

Vertical flights.—After Head-forward Displays, wild birds were often observed to make flights of three to five meters straight up into the air. These vertical flights were characterized by rapid wing-fluttering by both individuals. The birds were less than fifteen cm apart with legs and feet extended, beaks

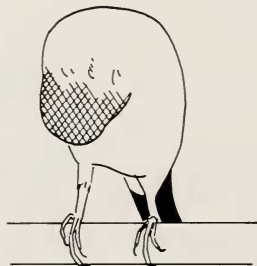


FIG. 6. "Displacement breast preening," front view.

open, and necks extended toward each other. At the completion of the encounter, the birds usually flew off with undulating flight. They sometimes chased each other, utilizing flapping flight and darting in and out through the dense foliage. These encounters occurred during the breeding season either on the feeding grounds or in nesting areas.

Avoidance reactions.—Since many of the agonistic postures are subtle, their identification sometimes depends solely on the reactions of submissive birds. These “avoidance” reactions are often inconspicuous. One of the best indications of avoidance is lateral presentation of the body to the aggressor; conversely, when a bird is likely to attack frontal presentation is the rule. As in the case in many fringillids (Hinde, 1955–56), submissive birds often assume a somewhat crouched posture, the legs being flexed to a greater extent than during normal perching. This is sometimes accompanied by a slight fluffing, especially of the crown feathers. Also indicative of submission is leaning away from an aggressor (Figs. 2 and 5). The head and/or tail are often bent away from the opponent. Keeping the neck withdrawn with the beak pointed downward (Fig. 5) again shows avoidance. Various combinations of these postures may be utilized.

Displacement activities.—Displacement activities, apparently unrelated behavior occurring before, during, or after agonistic encounters, are evident in the goldfinch and seem to indicate conflicting drives. As discussed previously (Coutlee, 1963), preening increases when agonistic behavior is at a peak. This preening, although including all regions of the body, is often concentrated near the head. Beak-wiping and head-scratching in particular are often observed during agonistic encounters. These movements are executed very rapidly by aggressive individuals just before or after displays and by submissive individuals after flight from an aggressor.

When conflicting drives of fear and feeding or fear and attack occur, the birds often assume a sleeked posture with legs extended, and neck extended

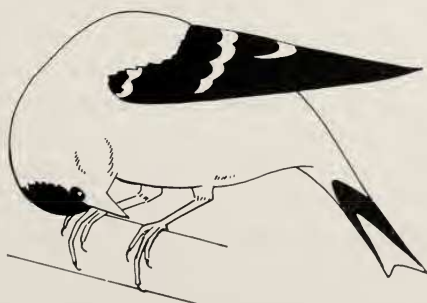


FIG. 7. “Displacement breast preening,” side view.



FIG. 8. Total aggressiveness for each month as evidenced by the average number of encounters per hour of observation (40 hr of observation).

and arched so that the beak points downward toward the abdomen (Figs. 6 and 7). This ritualized posture may be termed "displacement breast preening" and in caged birds it is sometimes followed by actual preening or pecking at the anal ring or crissum. During preening, however, the feathers are fluffed rather than sleeked. In wild birds, this same posture was seen when perching near a caged bird, prior to flight to the cage. In several cases, this was followed by pecking at the perch, and preening was never observed in this connection.

The agonistic displays described above have been observed, for the most part, under laboratory conditions. They occurred apparently at random in all parts of the cage. There are very few conflicts at the food source, in contrast to the behavior noted for the House Finch (*Carpodacus mexicanus*) (Thompson, 1960) and Chaffinch (*Fringilla coelebs*) (Marler, 1956). Aggression was noted at times toward an individual holding a leaf or nesting material, but in other instances two or three individuals pecked at the same object with no hostility. Supplanting was noted a few times in wild birds at feeding areas, but this only occurred during the nesting season when aggression was generally more evident. Agonistic behavior observed in connection with territoriality is discussed below.

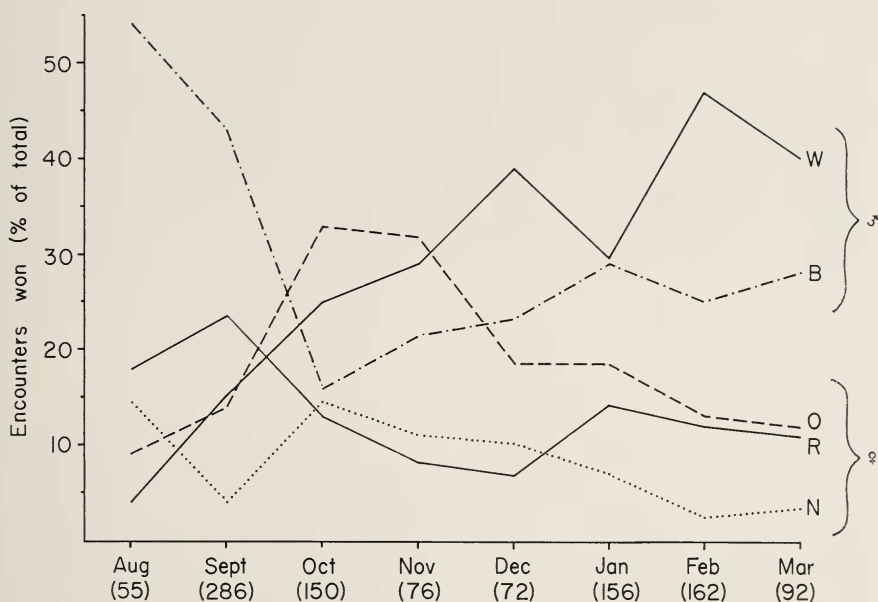


FIG. 9. Percentage of total encounters won by each caged bird for an eight-month period. Numbers in parentheses show total number of encounters per month (40 hr of observation).

AGGRESSIVENESS

Agonistic behavior in caged birds, under artificial conditions of lighting (12 hours light: 12 hours dark) was investigated. The intensity of this behavior each month, as indicated by the average number of encounters per hour of observation, is shown in Figure 8. Only eight months are included here. This permits consideration of only the months during which all five birds were together. Agonistic behavior was first observed on 24 August 1961 (30 days of age). Aggression was quite vigorous at this time and the number of encounters reached a peak during September, conceivably due to the crowding effect of the small cage. Transfer to a flight cage on 1 October was followed by a decrease in the number of encounters which was sustained throughout the winter months. Breeding plumage was attained quite early, perhaps as a result of the relatively long photoperiod during the winter. By January, early molt had produced an approximation of adult plumage. An increase in agonistic behavior was noted at this time and continued through 15 June when laboratory observations were terminated.

The relative aggressiveness of each bird was measured by tabulating the number of encounters won by each individual during one month as a percent-

TABLE 1
COMPARISON OF OBSERVED ENCOUNTERS WITH EXPECTED ONES

Month	Total encounters	Male-Male		Female-Female		Male-Female	
		Exp.	Obs.	Exp.	Obs.	Exp.	Obs.
August	55	6	7	17	15	33	33
September	286	29	37	86	72	172	177
October	150	15	11	45	22	90	101
November	73	7	9	22	24	44	40
December	72	7	14	22	17	43	41
January	157	16	55	47	33	94	69
February	162	16	66	49	13	97	83
March	92	9	19	28	10	55	63

age of the total number of encounters recorded for the month (Fig. 9). Individuals O, R, and N (as identified by color bands) were female, while W and B were male. Aggression during the first three months was quite variable, with individual hostility varying each month. After November, however, a definite trend is noted with males becoming more aggressive and females less. This trend becomes stabilized in January and remains constant throughout February and March. As pair bonds became stronger after separation of the birds into pairs in April, the females appeared to become more aggressive. For example, of the 50 encounters observed between paired individuals B and O, the female was the victor in 30 cases.

In order to determine the effect of sex on the incidence of agonistic encounters, the encounters were grouped as "male-male," "female-female," or "male-female." Assuming random meetings with three females and two males, the probable distribution of the types of encounters can be determined. For instance, any one female would be involved, during a given encounter, with one of two males and two other females. In other words, she would have equal chances of meeting with a male or a female. Likewise, a male would be expected to meet one of the three females in 75 per cent of his encounters. In Table 1, the actual number of encounters in each category each month is compared with this theoretical random number. It can be seen that observed values closely approximate those expected from August through November, while differences found in December are amplified through January, February, and March. Calculation of chi-square with a level of significance of 0.05 for two degrees of freedom shows that the encounters for the first four months can be considered as random. After this time, however, the encounters are definitely non-random. Variation from the expected values from December through March indicates an abnormally high percentage of male-male encounters, accompanied by a decrease in female-female and male-female en-

counters. If mere sex recognition through coloration were the criterion for determining encounters, then non-random aggressiveness should have been observed earlier, since the sexes were quite noticeably different in plumage during both October and November as well as the following months. Since these caged birds attained breeding plumage by January, it is probable that the change in behavior is a reflection of change in physiology as the breeding season approaches. These changes probably also occur in wild populations during competition between males for mates and/or territories at the beginning of the breeding season.

SOCIAL HIERARCHY

Social hierarchy, or "peck-order," was determined by examining conflicts between specific caged birds with regard to encounters won by each. A bird was considered to win an encounter when its activity evoked either a submissive display or flight by its opponent. Utilizing the information gained from the analysis of agonistic behavior between the sexes, encounters were grouped according to their occurrence during random or non-random months. Tables 2 and 3 show the combined data for these two periods. Individual birds are arranged according to apparent dominance as discussed below. The outcome of a conflict between any given pair of individuals shows considerable variation. For example, as seen in Table 2, B was the victor over W in 36 instances. W defeated B 28 times, however, even though B was on the whole the more dominant. The general trend is toward a straight-line hierarchy with males dominant to females. This may be represented as follows for the first four months:

TABLE 2
ENCOUNTERS WON BY EACH BIRD FOR RANDOM MONTHS

	B	W	O	R	N
B		36	54	63	41
W	28		43	21	13
O	32	14		45	27
R	33	17	13		39
N	19	4	6	19	

The number of encounters won by any given individual over each other bird is noted for the random months August through November. The table is read from left to right, the victors in the column to the left, losers along the top (e.g., B was the victor over W 36 times during the four-month period). Total encounters—567.

B (male)
 W (male)
 O (female)
 R (female)
 N (female)

As is evident by comparison with Fig. 9, the position in the hierarchy is influenced to some extent by the general aggressiveness of any one individual. Thus B, victor in a large percentage of encounters during August and September, appears as the dominant individual, while N is definitely subordinate, being the least aggressive of the group. On the other hand, the degree of individual aggression each month cannot be considered as entirely indicative of position in the hierarchy since, for example, O was generally more aggressive than W during the entire period, but appears beneath him in the hierarchy.

It must be remembered that this arrangement represents only an approximation of hierarchy for four months. Analysis of each month also shows frequent reversals in which individuals that are generally dominant are defeated by lower-ranking birds. In addition, triangles are often found in month-by-month analyses. For instance, in November O was dominant to R and R to B, but B was dominant to O. In other months, no dominance could be determined between two individuals, since they each won the same number of conflicts.

A similar analysis of non-random months gives the distribution shown in Table 3. The same trend is noted, with males dominant to females. In this case, however, a larger number of reversals was observed, and the group cannot be considered to possess straight-line dominance. The following arrangement gives an indication of the general trend, with arrows showing triangular relationships (\rightarrow) or lack of dominance (\leftrightarrow):



It will be noted here that the shifts occurring in the group all involve conflicts between the sexes. Thus, although the number of male-female conflicts is less than expected during these months (Table 1), changes in the hierarchy are confined to these encounters. This is perhaps an indication of an impending shift from male to female dominance during the breeding season. These findings are in accordance with Hinde's observation (1955-56) that fringillid females are generally dominant to males during the breeding season. Since the photoperiod was kept constant throughout the entire study with no increase in day length corresponding to natural increases in the spring, full

TABLE 3
ENCOUNTERS WON BY EACH BIRD FOR NON-RANDOM MONTHS

	W	B	O	R	N
W		133	16	34	19
B	32		31	26	48
O	27	14		20	20
R	12	26	6		20
N	18	8	7	2	

The number of encounters won by any given individual over each other bird is noted for the non-random months December through March. Total encounters—519.

breeding condition apparently was not realized by the caged birds. After initial investigation of cotton and excelsior supplied from April through June, the caged birds showed no inclination to use them for nesting purposes.

Paired females were observed to initiate vertical aggressive flights against their mates in the field, but supplanting of his mate by the male was observed to about an equal degree.

It may be concluded, then, that social hierarchy in the goldfinches studied tends toward male dominance in the winter and female dominance during the breeding season. These relationships are highly unstable, however, with many reversals and unpredictable outcomes. In general, the position in the hierarchy corresponds to relative aggressiveness of each individual.

TERRITORIALITY

The question of territoriality in the American Goldfinch is a controversial one. The possession of a territory is denied by Pitelka (1942) and Roberts (1942), those who agree on its occurrence differ in their analysis of its manifestation (Walkinshaw, 1938; Drum, 1939; Batts, 1948; Stokes, 1950; Nickell, 1951; Sutton, 1959), and some refrain from taking a stand at all (Nice, 1939).

In none of the papers mentioned above is the word "territory" used in the strict sense as a "defended" area. Perhaps this lack of consistency explains a portion of the controversy over territoriality in the goldfinch. If the ultimate criterion for territory-holding is overt defense, especially against members of the same species, then many of the descriptions of "territory" must be rejected as actually representing only the area most frequented by the birds in question.

Territoriality in the goldfinch does seem to exist to a limited extent, but its boundaries and methods of defense certainly render it a confusing phenome-

non at best. This is probably due to the extremely social nature of the species and the tendency to forage in flocks throughout the nesting season. A discussion of conflicts observed in breeding areas may aid in a partial understanding of this aspect of goldfinch behavior.

Formation and extent of territory.—The exact period of territory establishment is a controversial issue. Walkinshaw (1938) and Stokes (1950) indicate that territories are formed just before nest building begins. Drum (1939) contends that they are established "early in the nesting season" well before actual nest construction is under way. During observation periods by the author both in 1961 and 1962, several nests of a few fibers wrapped around forked branches were begun and then abandoned before the final nest was constructed. These differences of opinion thus may merely be a result of failure to find the inconspicuous partial nests, and territory may actually be formed well in advance of building of the final nest. In any case, pair formation seems to occur while the birds are in large flocks before or shortly after their arrival at the breeding grounds. This would indicate that a territory, if present, serves not to attract a mate but to insure isolation of a nesting pair.

In my own observations before nesting began, males were seen to give "song-flight" around favorite perching places, frequently large trees near feeding areas. These were followed by long bounding flights or chases between the males. Song-flight was terminated when the birds reached a distance of 50 to 100 meters from the point of its initiation. Two males which were captured and color-marked on 5 July 1962, were found at nests being constructed 15 and 65 meters, respectively, from the banding site on 14 July. In addition, one of these birds was seen to chase a second male from a dense dogwood clump where the final nest was constructed two weeks later. These observations suggest that, in these males, territory was formed at least two weeks before nest construction began. A female marked on 4 July was discovered nesting one mile distant on 9 July. This would indicate either that this female had not yet become associated with a definite nesting territory, or that if territorial tendencies existed, she still ranged a considerable distance from the prospective nesting area.

Although Walkinshaw (1938) found feeding areas within or near the territories, Drum (1939) observed that the birds travelled long distances to feed, and Sutton (1959) mentions the occurrence of both situations. In order to determine the extent of range in the goldfinches at the George Reserve, I banded and color-marked 28 birds from two weeks before to one week after nesting began. Twenty-one of these individuals were captured near a field where an abundance of ripe thistles (*Cirsium* sp.) and *Tragopogon* attracted large numbers

of foraging goldfinches. Observations after nesting was under way showed that, although the birds did at times feed within $\frac{1}{4}$ mile of the nest, they also returned to the field where they were first captured, about $\frac{1}{2}$ mile distant. Since (1) goldfinches could be found feeding there at almost any time of the day, (2) only about $\frac{1}{4}$ of them were marked, and these differently, (3) flights to and from the feeding area were in various directions, and (4) of eight pairs nesting in a marsh $\frac{1}{2}$ mile away, three individuals were found at the feeding area, it can be inferred that this field remained as an important foraging place for a large population of goldfinches even though nesting territories had been established.

Defense by the male.—True song, considered as an effective warning signal against other members of the same sex (Nice, 1941; Lack, 1943), was uttered only by males. It consists of an extended series of rapid notes similar to an un-accented *per-chic-o-ree* as given during flight, but at a faster tempo. This “twittering” is interrupted at frequent intervals by “squeals,” sliding notes either rising or falling in pitch; “sweet” notes, abruptly terminated squeals; and a rapid warble, described as “canary-like” by Drum (1939), Stokes (1950), Walkinshaw (1938), and others. The entire song is quite variable in both sequence and duration and is very loud. It is usually given from high trees near the nests but may also occur with flapping flight, resulting in the “song-flight” mentioned above. Stokes (1950) indicates that song in the American Goldfinch is “certainly associated more with courtship than with territory establishment,” basing this conclusion on the fact that males sang in flocks more than when alone and sang most frequently during courtship and before nest building had started. In the males under consideration here, however, loud, complex songs were frequently heard during the early stages of nest construction. In addition, lone males often sang loudly from high perches near partially completed nests. Since the sound carried for considerable distances and pairs had already been formed, song at this stage can probably be considered as advertising in function although it may, in addition, be a factor in maintenance of the pair bond.

During both summers of observation, circular flights of the male as described by Drum (1939) were noted in the vicinity of the nest sites. These were usually of the bounding type accompanied by a sharp *per-chic-o-ree*, but sometimes song-flight was given. These flights seemed to advertise the territory boundaries, but intruding males apparently were approached only when very close to the nest. The territory-holder then chased them using rapid flapping flight and emitting loud warbles and squeals as he darted in and out of the dense shrubbery near the nest.

Drum (1939) did not find males alighting within their own territories.

but they either circled them or perched near them in high trees. This was not the case among the birds studied in 1961 and 1962. These birds *did* show a tendency to perch and sing in trees at the edges of the area circumscribed by their circular flights. In addition, they perched quite frequently near the nest, especially during nest construction. This occurred whether or not the female was present. Males often perched quietly or preened in the tops of shrubs slightly higher than the nest tree and but 1½ to 3 meters away. Song was never heard from these perches, although soft warbles and squeals were sometimes given. Since no aggressive chases were begun from these perches, this behavior may indicate an interest in the nest itself rather than an expression of territoriality. Since the male is quite conspicuous, however, mere prominence may serve to intimidate other males.

Defense by the female.—Female goldfinches also show a tendency toward territoriality, but it is confined to the immediate vicinity of the nest. During nest construction, they fly to distances of ¼ to one mile away to gather nest materials, then return to the nest site, remaining near the nest when within their mate's territory. Close synchronization of the breeding cycles within any given population produces wide-spread nest construction with most of the females occupied with building at the same time. During incubation and brooding, females remain on or near the nest almost continuously and are fed by the male. Consequently, the females have little contact with each other after nesting begins. In combination with male territoriality, this leads to little intraspecific conflict involving the females during nesting. Other females alighting within about 5 meters of the nest are chased away, but this is usually evident only during nest building. The female appears to be generally more aggressive than the male during nesting, but since she seldom meets other goldfinches, this aggression is necessarily directed toward her mate or other species.

INTERSPECIFIC CONFLICTS

American Goldfinches caged with House Finches and Indigo Buntings (*Passerina cyanea*) showed little conflict with these species. Some aggression was observed, however, usually resulting in submissive displays or retreat of the goldfinches. On a few occasions, Head-forward threat displays were given toward House Finches, sometimes causing them to retreat. In most cases, however, the goldfinches were supplanted by these larger birds, either at the food dish or on the perches. The same was true of the buntings, again of larger size. Wild birds were seen feeding with Indigo Buntings without conflict, indicating that forced close association in aviaries may have resulted in the encounters between these species.

Interspecific conflicts among wild goldfinches primarily involved females,

and they usually occurred near the nest site. Conflicts observed in feeding areas at the George Reserve were confined to displays or chases by the females, directed toward Chipping Sparrows (*Spizella passerina*) which frequented the area.

During the early stages of nesting (construction of the nest through incubation of the eggs) the females were quite aggressive and chased Cedar Waxwings (*Bombycilla cedrorum*) and Catbirds (*Dumetella carolinensis*) from the vicinity of the nest. Smaller species, however, such as the Yellow Warbler (*Dendroica petechia*), American Redstart (*Setophaga ruticilla*), Yellowthroat (*Geothlypis trichas*), and Swamp Sparrow (*Melospiza georgiana*), were ignored even when they perched or sang near occupied goldfinch nests. As the breeding season progressed and young were being brooded or fed, the females became much more tolerant of the presence of other species, and conflicts were seldom seen.

In only one instance, during the early part of the nesting period, was a male seen to chase a bird of another species from a territory. A Cedar Waxwing alighted about 5 meters above the nest in a tree frequented by the male goldfinch. It was chased immediately from this perch by the goldfinch.

Supplanting or chasing of American Goldfinches by other species was not observed under field conditions.

DISCUSSION

Many of the components of the agonistic displays described above can also be seen in other, unrelated, behavior patterns. For example, wing-raising, lowering and extension of the neck, tail-flicking, and flexing of the legs may be recognized as components of take-off or flight intention movements. Hence, their presence in agonistic displays probably indicates the readiness to fly at an opponent. Some of these postures (for instance, flexing of the legs) are also seen in submissive individuals, and again probably indicate flight intention, in this case as an escape mechanism. Retraction of the neck is a preliminary to pecking and often occurs in agonistic encounters. This movement is completed if the opponent is actually attacked. These apparent relationships are similar to those described by Hinde (1955-56), Marler (1956), Dilger (1960), Thompson (1960), and others for other fringillids.

Avoidance reactions show tendencies toward calming of the aggressive individual through adoption of submissive postures. Keeping the side of the body toward the hostile bird not only shows lack of return aggression but presents a relatively well-protected surface to the attacker. The vulnerable head region is placed to the side as the aggressor faces the submissive bird, and the wing feathers are closest to its beak. Since pecking is directed toward

the nearest part of an attacked bird, lateral presentation is definitely advantageous and any pecks delivered fall on the relatively impermeable wings. Submissive birds often bend the head and neck away from the attacker. This response has been described for many species and is considered by Moynihan (1955) to be an intention movement of escape or avoidance. Of course, facing away from an aggressor serves to protect the eyes and facial region. In addition, the highly-contrasting black cap of the male is concealed, perhaps further contributing to the negative stimulus being presented.

Evidence of conflicting drives was shown during all agonistic displays. As suggested by Hinde (1955-56), hostile birds which do not actually peck show both fear and aggression. This seems to be the case in the goldfinch, since aggressive birds are often hesitant to attack, resulting in the displays described above. Raising of the crown feathers occurs in many cases in association with agonistic encounters and may be performed by either individual. This action seems to indicate fright or submission, since it often occurs while leaning away or turning the head away. It has also been seen repeatedly in birds captured in the field, when they are held in the hand during banding.

The agonistic displays in the American Goldfinch are, for the most part, characteristic of a large number of fringillids (e.g. Lesser Goldfinch (*Spinus psaltria*) (Linsdale, 1957); European Goldfinch, Greenfinch (*Chloris chloris*), Canary (*Serinus* sp.) (Hinde, 1955-56); Chaffinch (Marler, 1956)). The Head-up and Head-forward displays are often observed in birds which subsequently attack their opponents. There are differences, however, in the intensity and degree of utilization of these displays in the goldfinch when compared with other species. The extreme Head-forward Display was rarely seen during the winter but increased in occurrence as the breeding season advanced. Even when the birds approached full reproductive condition, however, these displays occurred infrequently, and both wild and caged birds fed in flocks with a minimum of conflict throughout the breeding season.

The submissive postures are also much more subtle than those found in some other fringillids. For example, the extreme "fluffed-submissive" posture of the Chaffinch (Marler, 1956) and European Goldfinch (Hinde, 1955-56) is almost non-existent in the American Goldfinch. It was only observed in subordinate individuals when extremely high intensity aggressive displays were given toward them.

The low intensity of the agonistic displays utilized by the American Goldfinch as compared with most other fringillids that have been studied may, of course, be due either to a genetically weak tendency to attack or to extremely effective appeasement or avoidance patterns (including passivity of the attacked individual). Although the displays are often subtle, it seems

unlikely that they are not correctly interpreted by other individuals of the species. Even a relatively low-intensity threat movement (i.e. Head-up or Carpals-raised) often causes flight of another bird. As noted above, submissive individuals usually lean away or turn the head away from the aggressor. This action serves to reduce the area of the conspicuous color patterns normally presented in attack postures (for example, the sharply contrasting black cap of the male) and thereby may inhibit the tendency of another bird to attack. Appeasement postures not only effectively control the action of the attacker by inhibiting its tendency to attack, but also cause no disturbance to other individuals nearby. In birds of a highly social nature, such as the goldfinch, this would certainly be advantageous to flock integrity during such activities as communal feeding. Linsdale (1957) has noted very little agonistic behavior in the Lawrence's Goldfinch (*Spinus lawrencei*) and suggests that inherently strong flocking tendencies may be responsible for this inhibition.

Displacement beak-wiping and head-scratching are often noted before, during, and after agonistic encounters and may be performed by either participant, as in most other passerines. In addition, the "displacement breast preening" posture is quite common in agonistic encounters and also appears in any "fearful" situation (close presence of an observer, approach to food dish already occupied by a superior, etc.). Although it is similar to the "displacement breast preening" of the Hawfinch (*Coccothraustes coccothraustes*), European Goldfinch (Hinde, 1955-56), and Greenfinch (Hinde, 1954), and is sometimes followed by preening, it may also be followed by pecking at the perch. It would seem that this movement may be derived from motor patterns related to feeding (fixation of seed or flower stalk directly below the body, pecking), preening (of abdomen, crissum, and anal ring), fleeing (extension of legs, sleeking of feathers), or a combination of these. The posture occurs only during situations characterized by conflicting drives of approach and flight.

It has been noted that House Finches (Thompson, 1960) and Chaffinches (Marler, 1956) show increased aggressive behavior at the food source. Marler (1957) found the same increase in aggression when a pair of siskins (*Spinus spinus*) was provided with a limited food source. In contrast, the captive goldfinches studied by the author showed almost no aggression at the food source throughout the winter months, even though all five often perched together on the small food dish (12 cm diameter) with but 1 to 5 cm separating each bird from its neighbor. Agonistic behavior at the food source increased as the breeding season advanced, but the number of encounters in all parts of the cage also increased at this time. It would seem, therefore, that although

in the goldfinch agonistic behavior is usually provoked by a factor such as violation of individual distance, which may occur at any point in space, the drives associated with feeding and/or flocking reduce this tendency to attack.

Although Roberts (1942) and Pitelka (1942) found no territoriality in the populations of American Goldfinches which they studied, the author has observed territoriality in the wild birds she studied, in accordance with the finding of Drum (1939). Since pair formation occurs while the birds are still in winter flocks, and since they usually forage in neutral areas which may be as far as $\frac{1}{2}$ mile from nest sites, the goldfinch territory functions mainly as a nesting area. The nests are fairly evenly spaced and, in the birds studied, were never less than 35 meters apart. This spacing is maintained by the males, each advertising and defending his territory by song flight. Occasional aggressive chases or actual fighting also occur within 5 meters of the nest. Linsdale (1957) has observed similar song flights and chases by male Lawrence's and Lesser goldfinches in the area immediately surrounding the nest. The female American Goldfinch may chase other birds, but usually this occurs only when they approach the nest site during early stages of nesting. The lack of rigid territorial defense in goldfinches as compared with other fringillids may be a result of their tendency to feed in neutral areas some distance from the nest. The selective advantage gained by holding a large territory including a food supply would thus be reduced. Conder (1948) indicates that the territory of the European Goldfinch becomes smaller after the eggs are laid. Since song flights and aggressive chases in the American Goldfinch decrease as the season progresses, its territorial boundaries seem merely to disintegrate rather than to actually recede.

Social hierarchy in the goldfinch is by no means a simple peck-right. The predictability of outcomes of encounters in stable straight-line or triangular hierarchies such as are found in domestic chickens (*Gallus gallus*) Schjelderup-Ebbe, 1922; Masure and Allee, 1934), Chaffinches (Marler, 1955), or Oregon Juncos (*Junco oreganus*) (Sabine, 1959) is lacking. Instead, during the winter months there are frequent reversals and unstable triangular relationships which may shift considerably from month to month. Shoemaker (1939) has found similar peck-dominance organization in captive flocks of Canaries, with daily or weekly fluctuations as well as some fairly stable relationships. This instability would suggest either great variation in aggressive drive or a lack of individual recognition. It seems unlikely that aggressive drive would be so variable since external conditions were constant and the internal milieu would be expected to be fairly stable at this time of year. Individual recognition would certainly be facilitated by the individual differences in calls and

songs noted during the breeding season. During the winter months, however, vocalization in captive birds is at a minimum and it may be that this results in a lack of recognition which leads in turn to the observed instability of social structure. On the whole, males are dominant to females during the winter, but since the sexes remain distinguishable throughout the year (at least to human eyes) this dominance would not necessarily depend on *individual* recognition.

As the breeding season approaches, females appear to become dominant to their mates. This occurrence is similar to that found in the Brambling (*Fringilla montifringilla*), Chaffinch, European Goldfinch, Greenfinch, Hawfinch (Hinde, 1955-56), and Canary (Hinde, 1955-56; Shoemaker, 1939), and also seems to occur in the Lawrence's Goldfinch and Lesser Goldfinch (Linsdale, 1957). Since female goldfinches do not encounter males other than their mates while actually incubating eggs or brooding young, and since the birds usually forage in flocks without conflict, there is little opportunity to observe agonistic encounters between females and males other than their mates during nesting.

SUMMARY

A study of behavior patterns in the American Goldfinch was conducted from March, 1961, through July, 1962. Observations of both caged and wild birds were integrated, and agonistic and related social behavior were discussed.

An analysis of displays observed during agonistic encounters indicate that Head-up, Carpals-raised, Head-forward, supplanting, and vertical flights are associated with aggressive drives. Fluffed and crouched postures, turning the head away, or leaning away show avoidance. Displacement activities include beak-wiping, head-scratching, and "displacement breast preening."

Encounters between caged birds were analyzed according to their implications with regard to aggressiveness and social hierarchy. Agonistic encounters were observed more frequently under crowded conditions and during the early portion of the breeding season than when adequate space was provided or during winter months. Males were generally more aggressive than females during the winter, with an apparent reversal at the onset of the breeding season.

The social hierarchy consists of a highly unstable peck-dominance, showing many reversals and triangular relationships, but with a tendency toward male dominance in winter months, female dominance during the summer.

Both sexes exhibit territoriality to a limited extent, at least at the beginning of nesting. An area of about 10 meters in diameter around the nest site is defended against other members of the species by chasing and fighting by the male, with display flights accounting for defense of an area about 30 meters in diameter surrounding the nest. The birds were found to range considerable distances from the nesting territories to forage. The female appears to be more often involved in conflicts with other species, apparently due to her increased aggressiveness during nesting combined with her isolation from other goldfinches.

The author's findings are compared with other recent studies of the behavior of fringillids.

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LITERATURE CITED

- BATTS, H. L., JR.
1948 Some observations on the nesting activities of the Eastern Goldfinch. *Jack Pine Warbler*, 26:51-58.
- CONDER, P. J.
1948 The breeding biology and behaviour of the Continental Goldfinch (*Carduelis carduelis carduelis*). *Ibis*, 90:493-525.
- COUTLEE, E. L.
1963 Maintenance behavior of the American Goldfinch. *Wilson Bull.*, 75:342-357.
- DILGER, W. C.
1960 Agonistic and social behavior of captive redpolls. *Wilson Bull.*, 72:114-132.
- DRUM, M.
1939 Territorial studies on the Eastern Goldfinch. *Wilson Bull.*, 51:69-77.
- HINDE, R. A.
1954 The courtship and copulation of the Greenfinch (*Chloris chloris*). *Behaviour*, 7:207-232.
1955-56 A comparative study of the courtship of certain finches (Fringillidae). *Ibis*, 97:706-745; 98:1-23.
- LACK, D.
1943 The life of the Robin. H. F. and G. Witherby, Ltd., London.
- LINSDALE, J. M.
1957 Goldfinches on the Hastings Natural History Reservation. *Amer. Midland Nat.*, 57:1-119.
- MARLER, P.
1955 Studies of fighting in Chaffinches. (1) Behaviour in relation to the social hierarchy. *Brit. Jour. Animal Behaviour*, 3:111-117.
1956 Behaviour of the Chaffinch (*Fringilla coelebs*). *Behaviour, Supplement*, No. 5.
1957 Studies of fighting in Chaffinches. (4) Appetitive and consummatory behaviour. *Brit. Jour. Animal Behaviour*, 5:29-37.
- MASURE, R. H., AND W. C. ALLEE
1934 The social order in flocks of the Common Chicken and the Pigeon. *Auk*, 51:306-327.
- MOYNIHAN, M.
1955 Types of hostile display. *Auk*, 72:247-259.
- NICE, M. M.
1939 "Territorial song" and non-territorial behavior of goldfinches in Ohio. *Wilson Bull.*, 51:123.
1941 The role of territory in bird life. *Amer. Midland Nat.*, 26:441-487.

NICKELL, W. P.

- 1951 Studies of habitats, territory, and nests of the Eastern Goldfinch. *Auk*, 68: 447-470.

PITELKA, F. A.

- 1942 High population of breeding birds within an artificial habitat. *Condor*, 44: 172-174.

ROBERTS, H. D.

- 1942 Some observations on the nesting habits of the Eastern Goldfinch (*Spinus tristis tristis*). (Unpublished MS, Univ. of Mich. Biological Station.)

SABINE, W. S.

- 1959 The winter society of the Oregon Junco: intolerance, dominance, and the pecking order. *Condor*, 61:110-135.

SCHJELDERUP-EBBE, T.

- 1922 Beitrage zur Socialpsychologie des Haushuhns. *Zeitschr. f. Psychol.*, 88: 225-252.

SHOEMAKER, H. H.

- 1939 Social hierarchy in flocks of the canary. *Auk*, 56:381-406.

STOKES, A. W.

- 1950 Breeding behavior of the goldfinch. *Wilson Bull.*, 62:107-127.

SUTTON, G. M.

- 1959 The nesting fringillids of the Edwin S. George Reserve, Southeastern Michigan (II). *Jack Pine Warbler*, 37:37-50.

THOMPSON, W. L.

- 1960 Agonistic behavior in the House Finch. Part I: Annual cycle and display patterns. *Condor*, 62:245-271.

WALKINSHAW, L. H.

- 1938 Life history studies of the Eastern Goldfinch. *Jack Pine Warbler*, 16:3-11.

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